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Aspects of the Fertilization Ecology of Broadcast Spawning Corals: Sperm Dilution Effects and *in situ* Measurements of Fertilization

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Abstract. A series of laboratory and field experiments was carried out to determine the effects of gamete dilution on fertilization rates in three species of reef coral. Gametes remained viable for 2 h after spawning, but one species exhibited signs of reduced fertility 3–4 h after spawning. Sperm dilution trials carried out in the laboratory indicated that fertilization reaches a maximum at sperm concentrations of 10^5–10^6 per ml, with reduced fertilization occurring at both higher and lower concentrations.

Estimates of "fertilization potential" in the field were obtained by exposing eggs to water samples taken from the field at various times and locations following episodes of coral spawning. This sampling program indicated that on nights when only small numbers of coral spawned (minor spawning), the fertilization potential was much lower than on major spawning nights. On major spawning nights, fertilization potential was consistently high just after spawning, but became spatially variable thereafter. The percentage of fertilization in field-collected samples of eggs and embryos just after spawning was also higher during major spawning nights than during minor spawning nights.

These measurements indicate that gamete dilution can play an important role in limiting the fertilization of coral eggs in the field during natural spawnings. It follows, therefore that corals are under considerable selective pressure to spawn synchronously in order to generate high gamete concentrations in the water column and thus to maximize the probability of successful fertilization. In addition to spawning in synchrony, corals also minimize the effects of gamete dilution by spawning buoyant gamete bundles that accumulate at the sea surface, and by spawning during periods of low water motion.

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Introduction

Fertilization is a critical and possibly limiting event in the life history of organisms that shed their gametes into the environment. Although behavioral phenomena such as spawning aggregations and synchronous gamete release are often presumed to have evolved as mechanisms to enhance fertilization (Giese and Pearse, 1974; Johannes, 1978; Babcock *et al.*, 1986; Pearse *et al.*, 1988), it is only recently that work on theoretical (Denny and Shibata, 1989) and actual (Pennington, 1985; Yund, 1990; Levitan, 1991; Levitan *et al.*, 1992) rates of *in situ* fertilization in broadcast spawning marine invertebrates have been studied. These studies suggest that gamete dilution in the field can result in very low fertilization rates, and that aggregation and spawning synchrony function to maximize fertilization. Working with echinoids in conditions of moderate current intensity, Pennington (1985) demonstrated that sperm concentrations and levels of fertilization rapidly decreased to low levels (<15%) at distances greater than 1 m from spawning males, and that sperm were short-lived. He concluded that gamete wastage due to the lack of successful fertilization could be significant in natural populations and that, though there was little consensus on whether aggregation is a characteristic feature of spawning echinoids, such aggregations could play a vital role in promoting fertilization. Similarly, Yund (1990) found that *in situ* fertilization of hydroid eggs during periods of calm water decreased substantially beyond 3 m from a source of sperm. In the brooding ascidian *Botryllus schlosseri*, Grosberg (1991) demonstrated that fertilization

from a known sperm [illegible] was reduced to negligible levels at distances of [illegible]50 cm. Recent work by Levitan (1991) and [illegible] (1992) has demonstrated that increases [illegible]ation size and aggregation can substantially [illegible]tilization success in sea urchins.

The model[illegible]ies by Denny and Shibata (1989) of gamete diffusion agree well with the experimental results mentioned above and suggest that, except in a very restricted set of circumstances, fertilization rates are likely to be extremely low. Nevertheless, the effectiveness of synchrony and aggregation behavior in ensuring high concentrations of sperm around eggs can be inferred from the presence of mechanisms that prevent polyspermy in the eggs of several echinoid species (Schuel, 1984).

Although the studies cited above have described fertilization rates achievable under specific experimental arrangements of male and female individuals (or discrete gamete samples acting as simulated individuals), few, if any measurements of fertilization rates have been made during natural spawning in an unmanipulated population. Such studies are essential in order to verify the existence of postulated strategies for increasing fertilization rates in environments where dilution effects are overwhelming.

The problems of gamete dilution are particularly acute in sessile organisms because their lack of motility precludes aggregation during spawning events. Thus sessile, broadcast-spawning organisms must rely on other mechanisms, such as synchronous spawning or aggregation during the settlement stage, to ensure fertilization. Probably the most spectacular example of synchronous spawning in sessile marine invertebrates is the annual mass-spawning of reef building corals on the Great Barrier Reef (Harrison *et al.*, 1984; Willis *et al.*, 1985; Babcock *et al.*, 1986; Oliver *et al.*, 1988) and in other parts of the Pacific (Heyward, 1988; Heyward *et al.*, 1987). On the Great Barrier Reef, over 130 species of coral are known to participate in this annual reproductive event, with over 30 species spawning on the same night (Willis *et al.*, 1985). These spawning episodes are highly predictable and, for many of the species involved, last for less than an hour every year. That corals synchronize their reproductive activities to this degree, even when such a strategy can lead to the loss of an entire year's reproductive effort through chance events such as heavy [illegible]ll (Harrison *et al.*, 1984), may reflect an overriding [illegible]chieve adequate concentrations of sperm and egg[illegible]ater column. Indeed, many of the hypotheses [illegible]pt to explain the timing of coral spawning [illegible]h as spawning predominantly on low neap t[illegible]nchrony have been concerned with the wa[illegible] this timing may optimize successful fertilization ([illegible] *et al.*, 1986).

In this study we investigate several aspects of the fertilization biology of mass spawning corals, with particular emphasis on factors that may influence successful fertilization in the field. We focus on three basic questions. (1) What is the optimal sperm concentration for fertilization of coral eggs? (2) How long after spawning do gametes remain capable of successful fertilization? (3) What is the spatial and temporal variability of fertilization in the field during nocturnal spawning events?

Materials and Methods

Study sites

Corals for these experiments were obtained from fringing reefs at two near-shore locations on the central Great Barrier Reef near Townsville, Australia (Fig. 1). The first of these sites was at Geoffrey Bay, Magnetic Island (19°10′S 146°51′E), where gametes were obtained from corals that spawned between October 27 and November 1, 1988, and October 16 through 18, 1989. The second site was at Pioneer Bay, Orpheus Island (18°35′S 146°29′E), where corals spawned one month later, between November 25 and 31 during both years.

Gamete collection

The species studied were *Montipora digitata*, *Favites pentagona*, and *Platygyra sinensis*. All three species are simultaneous hermaphrodites, releasing well-formed bundles containing both eggs and sperm (egg-sperm bundles). The eggs are highly buoyant and the bundles float rapidly to the surface where they break apart, usually within half an hour of release. If conditions are calm, the eggs, sperm, and associated mucus accumulate at the surface to form large, conspicuous "coral spawn slicks" (Oliver and Willis, 1987). Fertilization is not likely to occur until at least half an hour after spawning, since polar body extrusion does not occur before this time in faviids (*e.g.*, *Platygyra* and *Favia*) and may take even longer in acroporids (Babcock and Heyward, 1986).

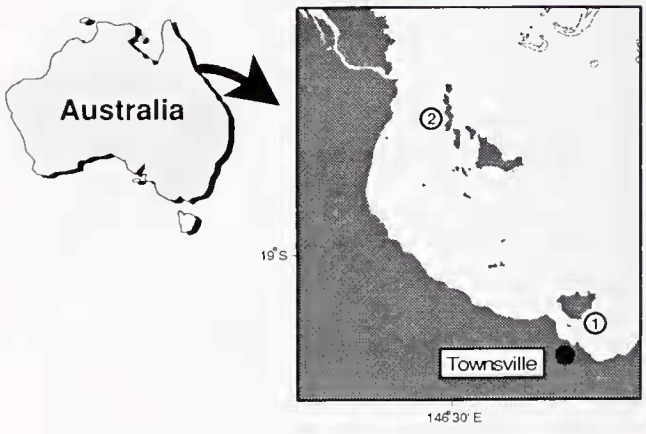

Figure 1. Map showing study locations at Geoffrey Bay, Magnetic Island (1) and Pioneer Bay, Orpheus Island (2).

The selected species all spawn on separate nights. In most species, spawning takes place on just one night, but in *M. digitata* spawning takes place over three nights, with the majority of spawning occurring on the second night (Heyward and Collins, 1985; Babcock *et al.*, 1986). Late in the afternoon on the day of spawning, ripe colonies were collected and placed, either in separate buckets, or in individual aquaria, with running water and aeration. The aquaria were left static after sunset to facilitate the collection of gametes.

The egg-sperm bundles used in these experiments were collected as soon as they reached the surface and were held in a small quantity of sperm-free seawater that had been collected in the afternoon, prior to spawning, about 1 km offshore from the island. The egg-sperm bundles were gently agitated at frequent intervals, until all the bundles broke apart, physically separating the eggs and sperm. This process took between 10 and 20 min. The eggs were then harvested with a wide-mouthed plastic pipette and rinsed to remove adherent sperm as follows.

The eggs were placed in 30 ml plastic vials, the bottoms of which had been replaced with 100 μ or 200 μ plankton mesh, depending on egg size. The vials then were partially immersed in sperm-free water, and the eggs were rinsed by agitation of the vial. After the rinse, the vials were rapidly transferred to a fresh volume of sperm-free water. This process was repeated nine times and the eggs were retained in the sperm-free water for later use. Each fertilization experiment included a set of washed eggs to which no sperm were added. This served as a control for either inadequate washing, or contamination by extraneous sperm. The original volumes of water in which the egg-sperm bundles were allowed to separate (approximately 300 ml), were used to provide concentrated sperm suspensions. Sperm concentrations in these undiluted suspensions were determined with a haemocytometer.

The first set of experiments carried out in 1988 resulted in a significant number of fertilized embryos which then developed abnormally. Subsequent trials with glass, polystyrene, and polycarbonate vials for egg-sperm incubations showed that, compared with glass, both types of plastic vial increased the proportion of abnormal embryos. Similar adverse effects caused by plastic have been reported by Dinnel *et al.*, 1987. All subsequent experiments in 1989 were carried out with glass vials. The vials were opened and soaked in seawater for 6 h before use.

Sperm dilution effects

The concentration of undiluted sperm was adjusted to about 10^7–10^8 ml $^{-1}$. These suspensions were then serially diluted 10 times (50% or 30% per dilution) in sperm-free water to provide a standard range of sperm concentrations (10^3–10^8 ml^{-1}). The sperm concentration was verified with a haemocytometer for one or two of the dilutions in each trial and was found to be within 10% of that predicted from the dilution factor. For each concentration, 25 ml of sperm suspension were added to three replicate 30 ml plastic (1988) or glass (1989) vials. These contained about 100 eggs in a small volume (<1 ml) of sperm-free water. Controls received the same volume of sperm-free water. The vials were sealed and placed in the sea where they received natural, irregular agitation. All egg-sperm combinations were carried out no more than 45 minutes after the serial dilutions were prepared. After three hours, the vials were retrieved from the sea, and the eggs scored to record the proportion which had been fertilized. All eggs that were at or beyond the two-cell stage were considered to have been fertilized.

Gamete age effects

Eggs of *Montipora digitata* and *Platygyra sinensis* were mixed with sperm at known concentrations at 30-min intervals to assess the potential longevity of gametes. The sperm concentration used was one that yielded the highest fertilization rates in initial trials. The sperm was stored at the dilution at which it was to be used, until the time the gametes were mixed. The protocol for sample preparation, incubation, and counting was the same as that described above for sperm dilutions. In these experiments, both eggs and sperm were allowed to age simultaneously. The effects of egg or sperm age could not be investigated separately.

Sperm concentrations in the field

Fertilization in the field was measured either by determining the percentage of fertilized eggs in the water column following spawning events, or by estimating the "fertilization potential" of discrete water samples taken at different times and locations around the reef. This second index was determined by incubating the water samples with washed eggs obtained from corals that had spawned in the laboratory. This assay allowed us to determine the likely percentage of eggs that would be fertilized by sperm in a particular water mass during times when very few eggs were present in the water. "Fertilization potential" thus provides a way of estimating the probability of successful fertilization for corals that spawn at a slightly different time or place than the majority of the population.

On the afternoon before spawning, two buoys were placed over the zone of greatest abundance of the coral species under investigation. The buoys were positioned about 250 m apart, parallel to the reef front. Divers monitored populations of *P. sinensis* and *M. digitata* for signs of spawning behavior (egg-sperm bundles can be observed within the colony before their release). As the first bundles

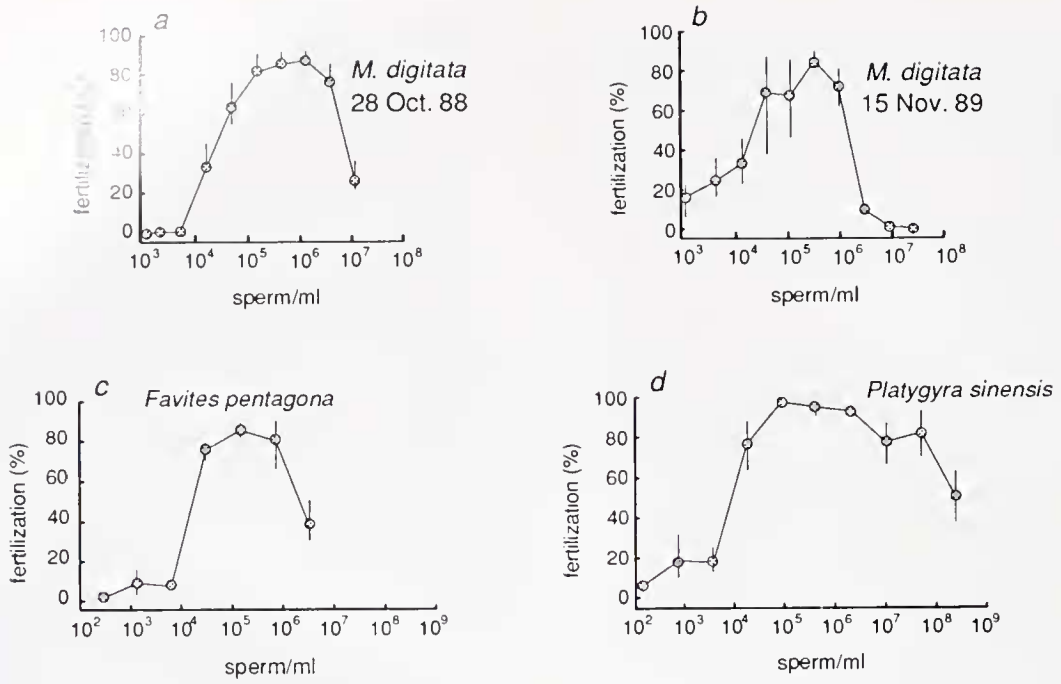

Figure 2. Sperm dilution series for *Montipora digitata* on two different nights (a, b), and for *Favites pentagona* (c) and *Platygyra sinensis* (d). Each series was run independently on separate nights. Values represent mean and ranges from three replicate vials.

were released, samples of seawater were taken from the surface adjacent to the buoys, and from the surface midway between them. The water samples were collected in 1 liter plastic bottles and transferred within 30 min to the laboratory where they were mixed with laboratory-spawned eggs in the manner described for the sperm dilutions. Although the field water samples occasionally contained some eggs, these were removed prior to mixing.

In an attempt to track patches of sperm near the surface during the hours after spawning, drogues ("X" vanes floating in the top 15 cm of the water column) were deployed above areas of actively spawning corals. Although these drogues track the near surface layer under calm conditions, they are not reliable indicators of water movement in the first few millimeters once wind speeds exceed 2–5 knots. As weather conditions during most spawning periods were calm, with occasional slight breezes, the drogues were used to increase the chances of finding patches of high sperm concentration. The drogues were tracked for several hours, and samples were taken both adjacent to (within) and between the drogues at 30–60 minute intervals.

During spawning of *M. digitata* at Magnetic Island in 1989, natural (*in situ*) fertilization rates were examined by means of a series of single neuston net tows made between drogues. In addition, dip samples were taken from any visible slicks of coral spawn that were encountered. Sampling with tows or dips was concurrent with the water sampling described above. The resulting eggs and embryos were subsequently preserved and counted.

Results

Sperm dilutions

Sperm dilution experiments were successfully carried out on three occasions with *Montipora digitata* and on one occasion each with *Favites pentagona*, and *Platygyra sinensis*. In all cases there was a broad optimum for fertilization at densities between 10^5 and 10^6 sperm/ml (Fig. 2). At concentrations below 1000 sperm/ml, fertilization rates were low. At very high sperm concentrations ($>10^6$ per ml), there is evidence of inhibition of fertilization, although this was less obvious in *Platygyra sinensis* (Fig. 2d).

Gamete age

The gametes of both *Platygyra sinensis* and *Montipora digitata* lost little viability for at least 2 hours after spawning (Fig. 3). Those of *Platygyra sinensis*, which were kept for a longer period (4.5 h) before being mixed, showed depressed levels of fertilization commencing at about 3 hours (Fig. 3). After about 3 hours, the eggs began to disintegrate, so no further viability studies were possible.

In situ *gamete concentrations and fertilization rates*

Fertilization potential of water samples. In 1988, water samples were taken on one night only, during a mass

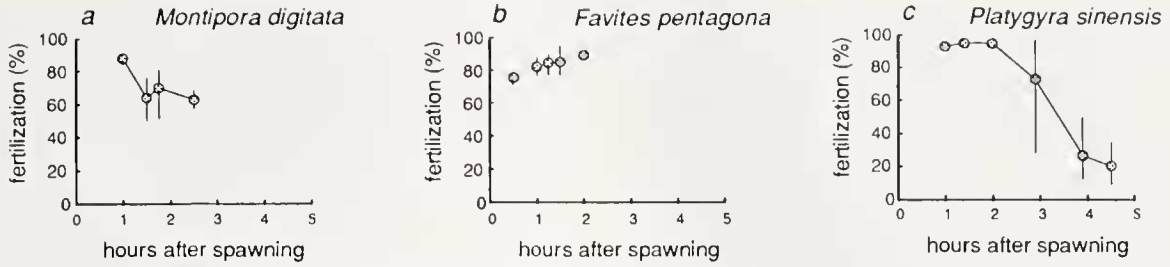

Figure 3. Gamete age effects. Fertilization rates (mean and ranges) for gametes of *Montipora digitata* and *Platygyra sinensis*, combined at varying times after spawning. Eggs and sperm were separated at the time of spawning and later re-combined with gametes from other colonies. Male and female gametes were of the same age at the time of mixing.

spawning event that included many faviid species. Weather conditions at the time of spawning were calm and the sea was glassy. During the first 1.5 to 2 h after spawning, large numbers of eggs from *P. sinensis* and other corals were visible at the sea surface around and near the drogues. The drogues moved slowly over the reef flat and were situated some 10–20 m off the edge of the reef by the time the last sample was taken 3.5 hours after spawning. The data in Figure 4 represent the pooled results from samples taken adjacent to, and midway between two drogues, since there was virtually no difference between the samples. Figure 4 clearly shows the fertilization potential for *Platygyra sinensis* rising to nearly 100% just after the initiation of spawning. During the next hour, rates were variable but slightly lower. By 3 hours after spawning, fertilization had dropped quite rapidly to near zero. This decrease is not due solely to an age effect, since it occurred earlier and was more pronounced than the reduction of fertilization observed in a concurrent longevity trial in the lab (Fig. 4). Samples were also taken from 1 m below the surface beginning 1.5 hours after spawning. These exhibited levels of fertilization very similar to the surface samples (Fig. 4), indicating that by this time the gametes were well mixed within at least the top meter of the water column. Statistical analysis of the results (Table I) indicate that by 1.5 hours after spawning, fertilization rates were significantly lower than those observed in the laboratory, and that fertilization decreased significantly in all treatments after 3 hours.

In 1989, seawater samples were taken over three consecutive nights during the spawning of *Montipora digitata* (Fig. 5). Fertilization rates were consistently low at all times and in all locations during the first and last nights of spawning. During the second night, which was the major night of spawning, fertilization rates were highly variable in space and time. For samples taken next to and between the two buoys anchored on the reef flat (Fig. 5c), fertilization rates were high at two of the three locations

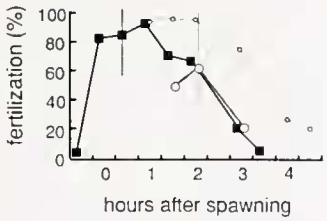

Figure 4. Fertilization rates for *Platygyra sinensis* resulting from water samples taken on the night of spawning. Each data point represents the mean and representative ranges of replicate vials (three sites each with three replicate vials). Time of spawning was determined by field observations. Solid squares: pooled results from single samples taken beside each drogue and midway between. Open circles: similarly pooled results from samples taken 1 m below the surface. Small circles and dashed line: results of gamete longevity trial using eggs spawned in the lab at the same time as the field, and a sperm concentration of approximately 500 sperm/ml.

Table I

(a) Two-way ANOVA for fertilization rates for Platygyra sinensis *samples at different times (1.5, 2, 3 h) after spawning and under different conditions (= Treatments: surface, 1 m,* in vitro*). The analysis was restricted to those times when all three treatments were sampled*

Source	df	SS	MS	F	*P*
Time	2	3296.2	6648.1	16.04	0.00
Treatment	2	7029.5	3514.7	8.48	0.002
Time × treatment	4	2548.9	637.2	1.54	0.233

(b) Tukey's Studentized Range test (HSD) α = .05; df = 18

Time/treatment level	Group	Mean	n
1.5 h	A	89.1	9
2 h	A	69	9
3 h	B	35.9	9
in vitro	A	87.2	9
surface	B	57.8	9
1 m	B	49.7	9

during the first hour but remained very low at all fixed locations thereafter. This suggests that eggs and sperm drifted off the reef flat during the first hour after spawning. Samples taken adjacent to, and between the two drogues (Fig. 5b) showed a similar pattern of initially high fertilization in two out of three locations followed by a rapid decrease. Two hours after spawning, only one drogue, located in a slick of eggs, was associated with high concentrations of sperm. By 3 h after spawning, fertilization was virtually zero for both drogues. But samples taken at this time from two ends of a surface slick of eggs, showed high rates of fertilization that were comparable to rates obtained in the lab with sperm at optimal concentration. Thus, after the first hour, high concentrations of sperm were found only in association with slicks (that occupy the first few millimeters of the water column), but were not consistently found next to drogues (which track the top 15 cm of water).

The difference in overall fertilization rates between the second night, when high rates of fertilization were obtained in some samples, and the first and third nights, when fertilization was consistently low, can be related to the intensity of coral spawning during this period. Table II shows

Table II

Percentage of Montipora digitata *colonies spawning on 14, 15 and 16 November 1989, compared to the percentage of fertilization from field water samples taken on the same night within an hour of spawning*

Date	% Spawning	% Fertilization (SD)
14th	16	1.01 (2.1)
15th	71	49.0 (37.3)
16th	3	0.2 (0.5)

Spawnings took place at Pioneer Bay, Orpheus Island. The same corals were observed each night, with some removal and replacement of stressed colonies. Numbers of colonies observed were: 14th, n = 15; 15th, n = 17; 16th, n = 12.

the proportion of colonies, collected for spawning studies, that spawned on each of the three nights. It can be seen that high fertilization rates occurred only on the night when a larger proportion of the colonies spawned.

Fertilization of eggs collected in situ. Fertilization rates of eggs in plankton samples taken from the sea surface in 1989 during the spawning of *M. digitata* at Magnetic Island reflected the same pattern as that seen over the three

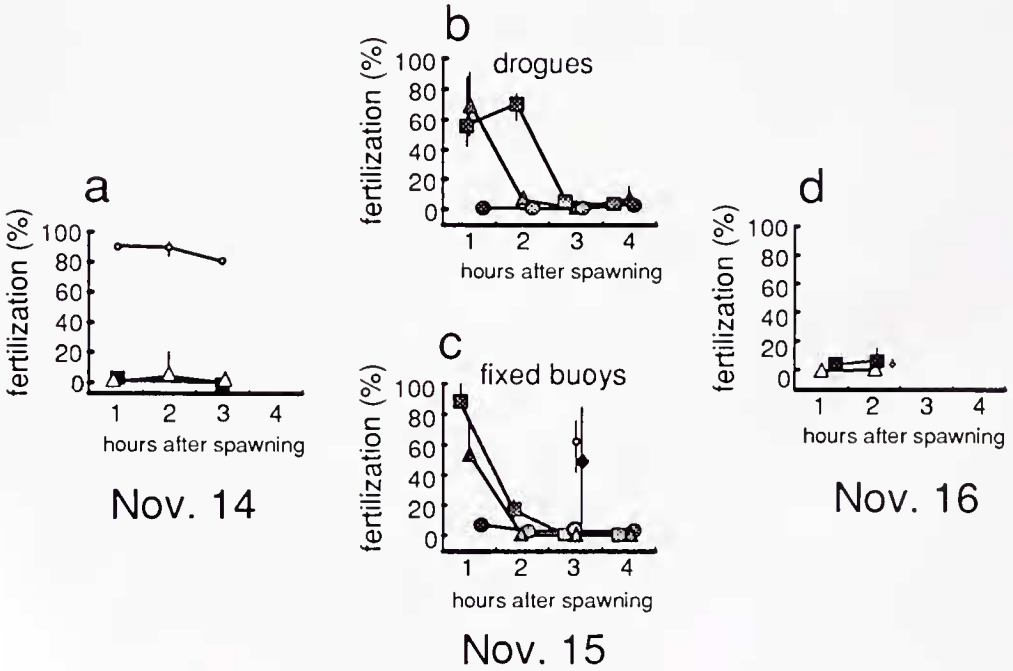

Figure 5. Fertilization rates resulting from water samples taken on the three major spawning nights for *Montipora digitata*, Orpheus Island in 1989. All error bars represent sample ranges. (a): Data for November 14th. Closed squares: pooled data from samples beside and between drogues. Open Triangles: pooled data from samples at and between fixed buoys on the reef flat. Small circles and dashed line: fertilization rates obtained in the lab with sperm at optimal concentrations. (b), (c): Data for November 15th (the major spawning night), showing results from each of three samples taken at (squares and circles) and between (diamonds) two drogues (b) and two fixed buoys (c). Diamonds show data from two samples (20 m apart) of the surface slick of eggs. Small circle shows results of a laboratory fertilization trial using optimum sperm concentration. (d): Data for November 16. Symbols as for (a).

nights of spawning at Pioneer Bay. We assume that the vast majority of these eggs came from *M. digitata* since this was the only species observed to spawn on the first two nights in question, and only one other species of *Montipora*, (restricted to the reef slope) was observed to spawn on the third night. With the exception of the genus *Porites* (which spawns 4–6 nights after the full moon), the eggs of *Montipora* can be distinguished from those of other corals by the presence of zooxanthellae.

Again, the highest rates of fertilization were recorded on the second night of spawning (Fig. 6), when large numbers of spawning colonies were observed by divers, and eggs were conspicuous at the water's surface throughout the sampling period. On the previous night, no spawning corals were observed by divers, and only a few eggs could be seen at the water's surface immediately after spawning. Fertilization rates were correspondingly low on this night, and on the last night, when winds were stronger. Although numerous colonies of *M. digitata* were seen spawning on the last night, only moderate numbers of eggs were seen on the water's surface after spawning, and no obvious concentrations were visible after that time. In Figure 6, the proportion of fertilized eggs appears to increase with time because cleavage is not initiated until 1–2 hours after spawning.

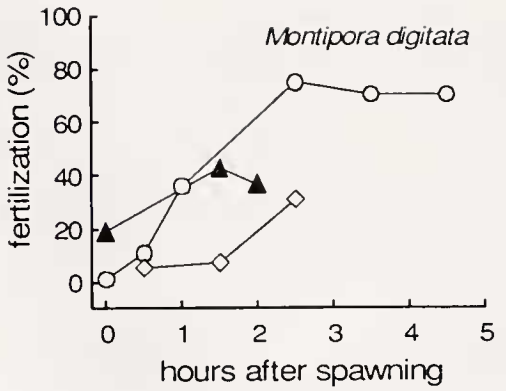

Figure 6. Fertilization rates for eggs of *Montipora digitata* obtained from plankton tows, Geoffrey Bay. Samples were obtained from single four-minute plankton tows during the nights of the 16th, 17th, and 18th of October 1989 at Geoffrey Bay, Magnetic Island (1st–3rd nights after full moon). Triangles: 16 October. Weather: winds 5–10 knots, some eggs seen in water immediately after time of spawning, but no spawning colonies observed in the field. Spawning itself observed only in aquaria. Circles: 17 October. Weather: winds 10 knots, many corals seen spawning and many eggs visible at the water's surface throughout sampling. Diamonds: 18 October. Weather: winds 10–15 knots. Many corals seen spawning. Moderate numbers of eggs visible after spawning but no obvious concentrations of eggs after this time.

Discussion

Fertilization rates of *Montipora digitata*, *Platygyra sinensis*, and *Favites pentagona* were all strongly influenced by sperm concentration, with optimal concentrations at about 10^5–10^6 sperm/ml. The pronounced decrease in fertilization rate at low sperm concentrations is presumably due to the decreased probability of successful egg-sperm encounters. Fertilization rates also declined at high sperm concentrations and were usually negligible above 10^7 sperm/ml. This reduction in fertilization rate may be due to the combined influences of decreased oxygen, increased CO_2, and lower pH. The inactivity of echinoid and ascidian sperm under these conditions is well documented (Chia and Bickell, 1983), and the existence, if not the cause, of this phenomenon has been known for some time (Lillie, 1915). Similar effects of high sperm concentrations on fertilization rates have been also reported for the bivalve *Mytilus edulis* (Ginzburg, 1975, cited in Sprung and Bayne, 1984). Our results therefore suggest that coral sperm are inactive when they are highly concentrated within egg-sperm bundles at the time of spawning, and that they are unlikely to be capable of full activity during the early stages of fragmentation of these bundles. This delay in the activation of sperm may be advantageous to corals for two different reasons. First, the delay may provide time for gametes from different colonies to mix, thus enhancing the chances of successful cross-fertilization. This would be especially important in those corals that are incapable of self-fertilization (Heyward and Babcock, 1986). Second, because Babcock and Heyward (1986) have shown that final egg maturation does not occur in many corals until 30 min after spawning, a delay in sperm activation would prevent energy reserves of the sperm from being expended prematurely.

Our experiments on gamete longevity indicate that the capacity for fertilization remains high for up to 2 h after spawning. In *P. sinensis*, where gamete viability was examined for a longer period, fertilization declined after 2 h, but remained substantially above zero (20–30%) for up to 4.5 h. Although the age of both eggs and sperm varied in these experiments, it is likely that the drop in fertilization rates with time probably reflects a progressive drop in sperm motility as the limited energy reserves in each sperm cell are depleted. Sperm respiration (and hence energy expenditure) is known to increase at low densities (Chia and Bickell, 1983), so the results presented here may not necessarily reflect the average longevity for gametes in the field, where more pronounced dilution effects could reduce the period of viability for most sperm.

Fertilization potential in the field exhibited several clear patterns. First, in both years of this study, there was a marked trend for high initial fertilization rates followed by a steady decline after 2–3 hours (Fig. 4). The decline was probably due to a combination of both dilution and ageing of gametes. Second, during 1989, when samples were taken over several nights, there was clear evidence

that the fertilization potential in the water column was drastically reduced on nights other than the principal spawning night, presumably due to rapid dilution of the small volume of gametes released on these nights (Fig. 5, Table II). During the major spawning nights, the concentration of sperm was patchy, and enhanced levels of fertilization were found for a much longer period in certain drifting patches than in areas over the reef flat where spawning occurred (Fig. 5b, c). These patches of high fertilization potential (*i.e.,* high sperm concentration) were invariably associated with concentrations of eggs and embryos (coral spawn slicks) at the sea surface.

The principal conclusions to be drawn from these results are that high sperm concentrations are important for successful fertilization, and that this is most effectively achieved by synchronization of the spawning event. Individuals that spawn either on a different night, or at a different time from the main spawning event, are clearly disadvantaged by a substantial reduction in the probability of successful fertilization of their gametes. The results of the *in situ* sampling of eggs during 1989 also support this conclusion since the percentage of fertilized eggs obtained from surface tows was twice as high during the main spawning night as on other nights.

The critical role that gamete concentration plays in the successful fertilization of marine organisms has been highlighted by the theoretical models of Denny and Shibata (1989), and by empirical studies on sea urchins, hydroids and ascidians (Pennington, 1985; Levitan, 1991; Levitan *et al.,* 1992; Yund, 1990; Grosberg, 1991). All of these studies showed that gametes are rapidly diluted and that fertilization is very low unless some means of creating high gamete concentrations is used.

High concentrations of gametes can be created and maintained in a number of ways during spawning events. These include: aggregation of spawning individuals; gregarious settlement of sessile organisms, resulting in high concentrations of spawners once sexual maturity is reached; spawning during periods of low water volume or low water exchange; and production of gametes that tend to resist dispersal in one way or another. For sessile invertebrates, such as corals, the options are somewhat restricted because adults cannot aggregate at the time of spawning. In contrast to many intertidal species, they are usually confined to a restricted or densely populated stratum. Sessile invertebrates such as crinoids (Kubota, 1989) and polychaetes (Caspers, 1984) commonly achieve high levels of gamete concentration through the synchronization of their spawning behavior, and this is clearly a mechanism exploited by corals (Willis *et al.,* 1985; Babcock *et al.,* 1986; Richmond and Hunter 1990; this paper). In addition, many corals overcome their lack of mobility by spawning buoyant egg-sperm bundles that may themselves aggregate at the surface of the sea. In these aggregates, gametes are much more concentrated than they would be if they were spread throughout the water column. A similar effect is achieved in polychaetes through the swarming of epitokes at the sea surface (Caspers, 1984). Furthermore, in corals, mucus associated with the testes acts to bind the spawned material together in a surface slick that resists dispersion by wind and waves (Oliver and Willis, 1987; pers. obs.). Finally, corals on the Great Barrier Reef tend to spawn during the falling tide of a neap cycle, when the dispersive effects of tidal currents are at a minimum, and when the volume of water over the reef flat is reduced for a prolonged period. Thus corals appear to have evolved a number of behavioral and physical adaptations to overcome the problem of gamete dilution in the ocean.

Although the need to achieve high concentrations of gametes after spawning may underlie the high level of synchrony that exists within each coral species, it does not explain why so many different species should spawn on the same night of the year (Harrison *et al.,* 1984; Babcock *et al.,* 1986). Indeed, there would appear to be some disadvantage in spawning at the same time as other congenerics due to an increased probability of producing inviable hybrids (Hodgson, 1988).

Although our results suggest that quite high levels of fertilization occurred in the field during the main spawning nights, these field observations should be repeated when weather conditions are less calm. If most spawning occurs on a night when the winds are high, then the resulting wave action would cause a much higher degree of vertical mixing of the buoyant gametes. This would probably reduce both post-spawning gamete concentrations, and fertilization rates below those observed in the present study. In species that rely on the concentrating effects of buoyant gametes, weather may play a critical role in determining fertilization rates and the success of spawning for any one year.

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